LEAF ANGLE AND LIGHT ABSORPTANCE OF ARCTOSTAPHYLOS SPECIES (ERICACEAE) ALONG ENVIRONMENTAL GRADIENTS

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The purpose of this research was to test the hypothesis that changes in leaf energy balance characteristics are correlated with the distribution of *Arctostaphylos* Adans. species along environmental gradients. It was expected that species from low light, low temperature environments should hold their leaves more horizontally and absorb more light than leaves of species from warmer, high insolation areas. Similar results have been reported by Billings and Morris (1951) for leaf reflectance and by Mooney *et al.* (1971) for leaf angle distributions of groups of shrubs from different habitats. The present research differed from these studies in that it involved a more detailed comparison within a single genus.

There are over fifty recognized taxa of *Arctostaphylos,* nearly all of them confined to the west coast of North America. All are woody evergreen shrubs with flat leaves (Munz 1959, Adams 1949). About half of the species are highly localized endemics (Stebbins and Major 1965). Seven species of *Arctostaphylos* were studied in the field at 54 sites in California, Oregon, and Washington. The sites and species were chosen for their distribution along two macroclimatic gradients of air temperature and insolation. These climatic gradients were associaited with elevational changes in the Sierra Nevada of California, and with latitude and distance from the seacoast in northern California, Oregon, and Washington. Climatic information was obtained from the *Climatic Atlas of the United States* (U. S. Environmental Sciences Administration, 1968), the *U. S. National Atlas,* and *Climates of the States* (U. S. NOAA, Dept. of Commerce, 1973).

Methods

Leaf angles were measured using a protractor to which a plumb line was attached at the origin (Kvet and Marshall 1971). The protractor was held up to the leaf and the angle between the leaf and the horizontal was measured to the nearest 5°. For these flat leaves, angle to the horizontal was considered to be the steepest angle that could be measured and did not take into consideration the azimuth angle, leaf-branch angle, etc. This method was found to give rapid, highly repeatable results. Angle measurements were made throughout the canopy of the shrubs examined,

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usually 10–20 leaves from each of several branches per shrub, 3–10 shrubs per site.

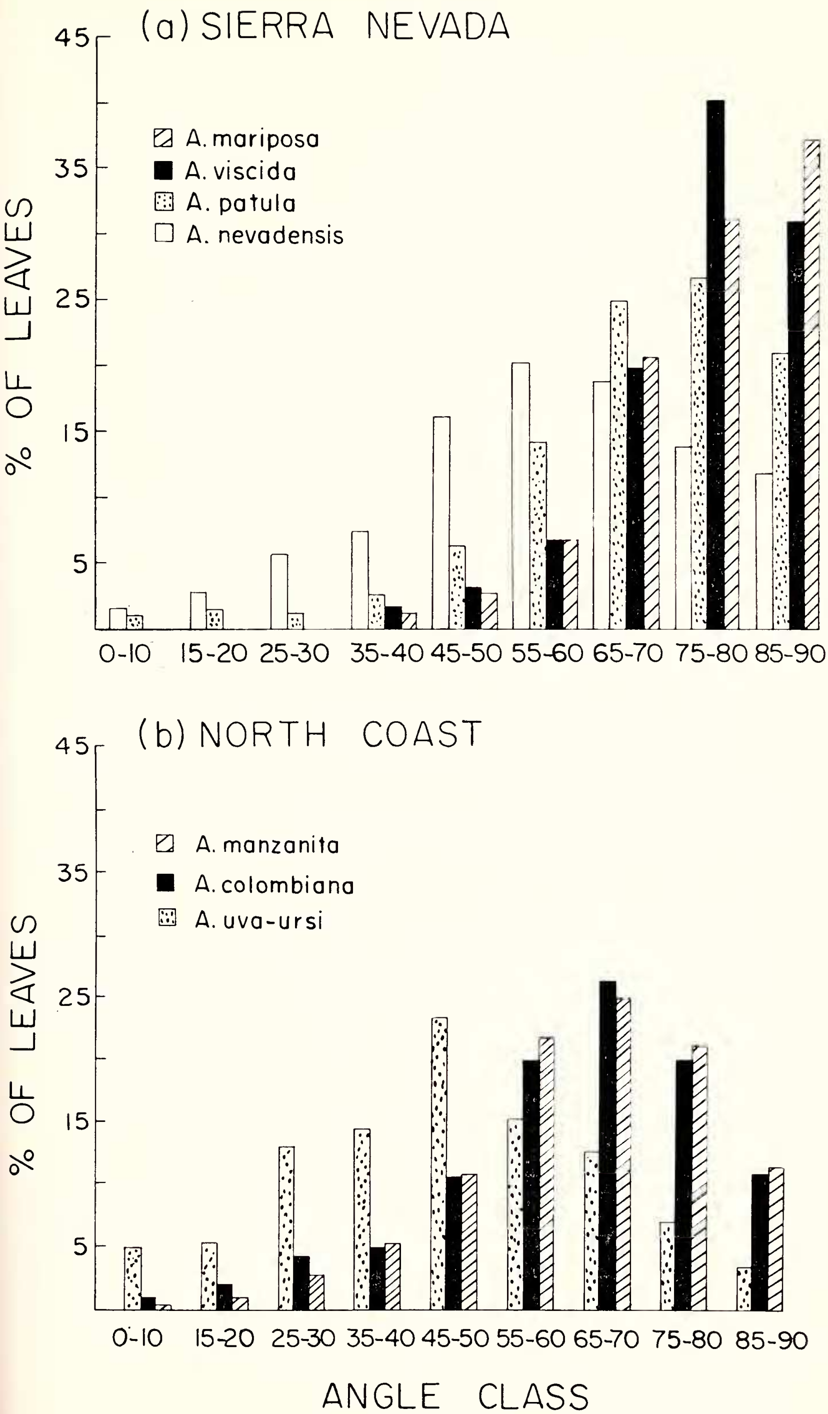
Reflectance and transmission of *Arctostaphylos* leaves were measured using a Zeiss PMQII spectrophotometer with reflecting sphere attachment. Absorptance was then calculated as: Absorptance = 1 − (Reflectance + Transmittance). All values were calculated as percentages, either of reflectance from a standard $MgCO_3$ block (reflectance) or of transmittance measurements taken with no obstructions between light source and sensor (transmittance). Measurements between 325 and 800 nm were taken using a photomultiplier tube as a sensor, while a PbS photocell was used between 700 and 2500 nm, with a 100 nm overlap between sensors. Variation among leaves at a single wavelength was rarely greater than 5%, and repeated measurements of the same leaf varied by less than 1%. In most cases, reflectance and transmittance were measured for at least six leaves of each species at each wavelength.

Results and Discussion

Figure 1a and Table 1 summarize the results of leaf angle observations at 29 sites between Yosemite National Park and Truckee, California. The data show that *A. nevadensis,* the species from the highest elevation sites, has many fewer vertical or near vertical leaves than *A. viscida* or *A. mariposa,* the two lowest elevation species. *Arctostaphylos patula,* the species from middle elevations in the Sierra Nevada, is intermediate in its leaf angle distribution.

Similar results are recorded in Figure 1b. *Arctostaphylos uva-ursi,* which is circumboreal in its distribution, was measured at three sites in Mason and Kitsap counties, Washington, and Curry County, Oregon. On these sites, *A. uva-ursi* grows between 10 and 100 m elevation, rarely more than 1 km from the ocean. *Arctostaphylos columbiana,* which was sampled at the same three sites plus another in Humboldt County, California, grows above *A. uva-ursi* to 800 m in the Pacific coast ranges. *Arctostaphylos manzanita* grows mainly in the interior coast ranges and was sampled in Humboldt and Mendocino Counties, California, at two sites about 50 km from the coastline. The data of Figure 1b show that *A. uva-ursi,* the species from the cool, foggy, coastal habitat, holds its leaves most nearly horizontal, and that leaf inclination tends to increase with distance from the ocean. Leaf inclination of *A. manzanita* is not as steep as in *A. mariposa* (Fig. 1a, Table 1), but growing season temperatures and insolation are much lower in the northern California coast ranges than in the Southern Sierran foothills (*Climatic Atlas of the United States,* U. S. Environmental Sciences Administration, 1968).

Fig. 1. Relative frequency of leaves in various leaf angle classes in the Sierra Nevada and Coast gradients. α = mean of all measurements.



(a) SIERRA NEVADA
A. mariposa
A. viscida
A. patula
A. nevadensis
% OF LEAVES
45
35
25
15
5
0-10
15-20
25-30
35-40
45-50
55-60
65-70
75-80
85-90
(b) NORTH COAST
A. manzanita
A. colombiana
A. uva-ursi
% OF LEAVES
45
35
25
15
5
0-10
15-20
25-30
35-40
45-50
55-60
65-70
75-80
85-90
ANGLE CLASS

TABLE 1. ELEVATIONAL RANGES, MEAN LEAF ANGLES FROM THE HORIZONTAL (α), COS α, AND MEAN LIGHT ABSORPTANCE IN THE VISIBLE AND NEAR-INFRARED REGIONS FOR THE SPECIES USED IN THE PRESENT STUDY. Values in parentheses indicate sample size.

	Elevation, m	α	cos α	Mean absorptance, % 400–675 nm	Mean absorptance, % 800–1100 nm
Sierra Nevada					
A. mariposa	150–1500	77.35 (420)	.22	—	—
A. viscida	150–1500	76.24 (460)	.24	78.96	4.01
A. patula	1000–2800	69.72 (1260)	.35	86.58	4.35
A. nevadensis	1700–3500	50.97 (1030)	.63	83.83	4.89
North Coast					
A. manzanita	200–1500	62.83 (320)	.46	—	—
A. columbiana	50– 800	62.01 (720)	.47	87.97	8.01
A. uva-ursi	10– 100	47.51 (410)	.68	91.87	8.67

In addition to the differences in leaf orientation, there are also differences among species of *Arctostaphylos* in light absorptance, particularly in the visible region (Fig. 2, Table 1). *Arctostaphylos viscida,* the species from the warmest, highest insolation environment, absorbs much less visible radiation than any of the other species. *Arctostaphylos uva-ursi,* from the foggy coastline, clearly absorbs the most light between 25,000 and 15,000 wave numbers (400–675 nm). The intermediate species, *A. patula* and *A. columbiana,* are intermediate in their visible light absorptance characteristics. *Arctostaphylos nevadensis* is the only species that contradicts the predictions of the original hypothesis. This anomaly may be related to the frequently very high radiation intensities during the growing season at the high elevations where *A. nevadensis* is found. In the near infrared region, all three of the Sierran species absorb about half as much radiation as the Coastal species.

Differences among species in light absorption are much smaller than those for leaf orientation (Fig. 1, 2), suggesting that leaf orientation is much more important than absorptance in regulating the energy balance of *Arctostaphylos* leaves. Lack of precise correspondence with the predictions for absorptance of the original hypothesis therefore may not be critical. In general, however, the predictions of the hypothesis are validated for leaf angle and for light absorptance of at least the two extreme species, *A. viscida* and *A. uva-ursi.*

Several other factors also might tend to counteract the predicted trends. For example, leaves of both *A. uva-ursi* and *A. nevadensis* are the smallest among all species studied, usually less than 2.5 cm long by 1.5 cm wide. Leaves of *A. viscida* may be over 4.0 cm long and 4.0 cm wide. If large leaves tend to have greater leaf-air temperature differences, the advantages of near vertical leaves and low absorptance may be counteracted. Field measurements of leaf temperature and photosynthesis are

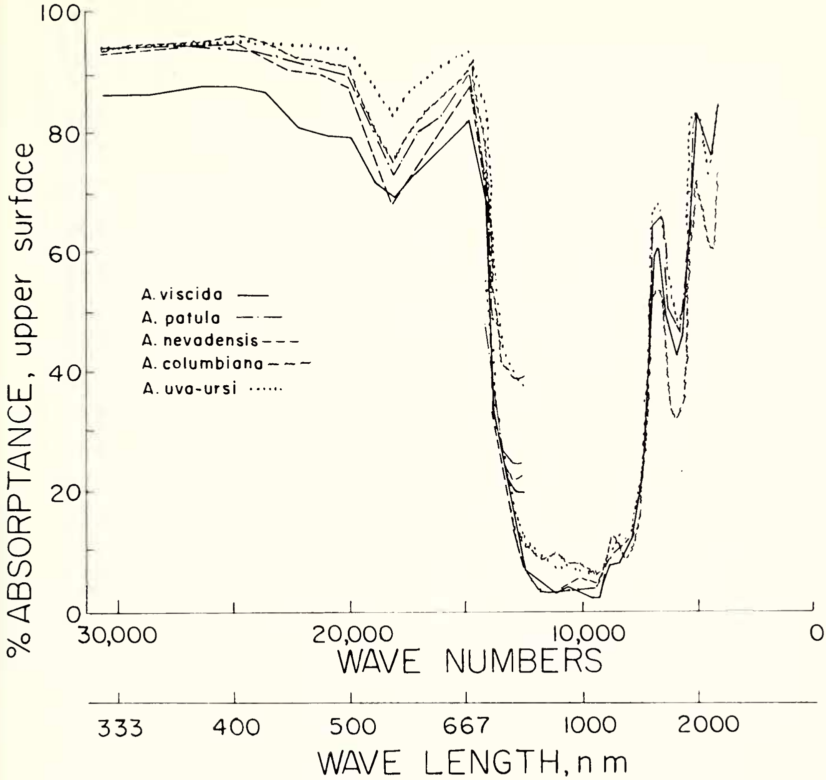


Fig. 2. Percent of incident light absorbed by leaves of *Arctostaphylos spp.* Wave numbers are used in the abscissa of this plot in order to emphasize the shorter, high energy wavelengths.

needed. This research also has not considered the importance of canopy structure on light absorptance and leaf temperature. *Arctostaphylos* appears to be a genus of plants very well suited to future studies of adaptation to radiation and temperature in the environment.

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LITERATURE CITED

ADAMS, J. E. 1940. A systematic study of the genus *Arctostaphylos* Adans. J. Elisha Mitchell Soc. 56:1–62.

BILLINGS, W. D. and R. J. MORRIS. 1951. Reflection of visible and infrared radiation from leaves of different ecological groups. Amer. J. Bot. 38:327–331.

KVET, J. and J. K. MARSHALL. 1971. Assessment of leaf area and other assimilating plant surfaces. In: Z. Sestak, J. Catsky, and P. G. Jarvis, eds. Plant photosynthetic production: Manual of methods. W. Junk, The Hague.

MOONEY, H. A., S. L. GULMON, D. J. PARSONS, and T. F. HARRISON. 1976. Morphological changes within the chaparral vegetation type as related to elevational gradients. Madroño *22:* 281–285.

MUNZ, P. A. 1959. A California flora. University of California Press, Berkeley.

STEBBINS, G. L. and J. MAJOR. 1965. Endemism and speciation in the California flora. Ecol. Monogr. 35:1–35.

NOTES AND NEWS

NOTES ON TWO RARE, ENDEMIC SPECIES FROM THE KLAMATH REGION OF NORTHERN CALIFORNIA, PHACELIA DALESIANA (HYDROPHYLLACEAE) AND RAILLARDELLA PRINGLEI (COMPOSITAE). — *Phacelia dalesiana* J. T. Howell was originally described from a population in the Scott Mountains at what is now Scott Mountain Summit on Highway 3 in Trinity County (Howell, J. T., 1937. Leafl. W. Bot. 2:51–52). The second known locality for this species was found 31 km to the south in the Trinity Alps (7 July 1975; *J. M. Di Tomaso 109,* DAV). The population consists of 700–1,000 individuals and is scattered in open Red Fir Forest at 2,011 m along the trail from Deer Flat to Shimmy Lake, 9.6 km WNW of Trinity Center; T36N, R8W, Section 5, NW-¼ (41°0′50″N, 122°48′40″W). Additional specimens have been deposited at CAS, HSC, and JEPS (8 July 1976; *Ferlatte and Di Tomaso 1776*).

Raillardella pringlei Greene was first collected by Pringle in 1881 from the "mountains about the head waters of the Sacramento River" in Siskiyou County and described by E. L. Greene (Bull. Torrey Bot. Club 9:15–17, 1882; isotype: CAS!). It has also been collected in the same general area near Gumboot Lake 12 km south of Mt. Eddy (*D. Barbe 538,* CAS, JEPS). Ferlatte (*A Flora of the Trinity Alps of Northern California,* Univ. Calif. Press, Berkeley, pp. 50–51, 1974) reported this species from Union Creek and Landers Creek in Trinity County at elevations from 6,500–7,200 ft. (1980–2195 m). Further field work in the Trinity Alps has shown *Raillardella pringlei* to be relatively common in the Swift Creek drainage and to occur as low as 1,295 m (*J. Di Tomaso 640,* CAS, DAV, and HSC). J. L. Strother obtained chromosome counts of $2n = 17$ II from populations on Union Creek *(Ferlatte 1805, 1806)* and Landers Creek *(Ferlatte 1812).* Vouchers have been deposited at HSC, JEPS, RSA, and UC. In all cases where *Raillardella pringlei* has been observed in the field it occurs in wet places such as stream banks or boggy areas, usually among serpentine rocks or in soils derived from serpentine or related ultramafics. Associated genera include the following: *Darlingtonia, Caltha, Schoenolirion, Carex, Adiantum,* and *Dodecatheon.* I thank Joseph M. Di Tomaso and John L. Strother for their contributions to the data presented here. — WILLIAM J. FERLATTE, California Dept. of Agriculture, 3288 Meadowview Rd., Sacramento, CA 95832.